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Inheritance in oat (*Avena sativa* L.) of tolerance to soil aluminum toxicity

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ABSTRACT - *Aluminum toxicity is a limiting factor for the expression of the yield potential in oat. The development of aluminum toxicity-tolerant genotypes is the cheapest and most feasible alternative for cultivation of soils with acid subsoil. Objectives of this study were to determine the gene action, number of genes and heritability of tolerance of oat genotypes to toxic aluminum concentrations. Parent genotypes and the F_1 and F_2 generations of some crossings plus the F_3, F_4, F_5, BC_1F_1, and BC_2F_1 generations were discriminated by the analysis of root regrowth in plantlets exposed to aluminum. Additive gene action predominated among the genetic effects. Only one segregating gene was found which has multiple alleles, two for tolerance (Al_1 and Al_2) and one for sensitivity (al). The heritability of the trait was high, indicating that tolerant genotypes can be selected in early generations of improvement programs.*

Key words: Oat improvement, acid soils, roots, genotypes, heritability.

INTRODUCTION

Aluminum toxicity is a limiting factor for the full expression of the yield potential of crops grown on many soils around the world. An alternative solution to this problem is liming. But even where the arable layer can be corrected, the correction of the subsoil is economically unfeasible, leading to a reduced root penetration in this region which diminishes the water supply, mainly in soils cultivated without irrigation or with a lower water retention capacity.

The species and cultivars differ widely in tolerance to aluminum in toxic concentrations in the soil. It has been demonstrated that this tolerance is a genetically controlled trait and can consequently be improved.

Aluminum toxicity is more severe below pH 5.0, but can occur even at values above pH 5.5. The critical pH value for the plant at which Al^{+++} becomes soluble and toxic depends on several factors such as the clay type, organic matter content, other cation and anion concentrations, and total salts (Foy et al. 1978, Nodari et al. 1982).

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Symptoms of aluminum toxicity in roots are shortening and thinning at the tips, inhibiting the formation of fine root ramifications and leading to inefficient water and nutrient uptake. These effects are probably linked to the inhibition of elongation and cell division. The soil volume explored by roots consequently shrinks. Foy and Fleming (1978) suggest the inhibition of root development as a biological indicator in the selection process of plants tolerant to toxic aluminum concentrations in the soil.

Nutrition solutions have been used to discriminate tolerant from non-tolerant populations in gramineous species such as oat (Sánchez-Chacón et al. 2000, Gotuzzo et al. 2001, Wagner et al. 2001), wheat (Camargo and Oliveira 1981, Camargo 1984, Dornelles et al. 1996) and barley (Minella and Sorrells 1992). Results obtained with solutions agree with those obtained in soil, showing clearly that an evaluation in nutrition solution effectively identifies the tolerance levels for a large number of genotypes, and is recommended as auxiliary technique for improvement programs.

Cereals differ greatly in their responses to the presence of aluminum in the soil. Oat is more tolerant to soil acidity than wheat and barley but less tolerant than rye (Camargo and Felício 1984).

For oat, Sánchez-Chacón et al. (2000) concluded that the trait tolerance to toxic aluminum level is an inheritable trait, controlled by one gene and with dominant gene action. Wagner et al. (2001) evaluated a larger number of crossings and obtained results indicating the presence of one or two dominant genes involved in aluminum tolerance.

The present study had the objective to determine the gene action and estimate the number of genes and heritability of tolerance to aluminum toxicity of oat genotypes.

MATERIAL AND METHODS

Four oat genotypes with differential response regarding tolerance to aluminum toxicity were included in our study (Table 1). Three genotypes were selected from the Genetic Improvement Program for Oat of the UFRGS, based on data obtained by Sánchez-Chacón et al. (2000) and Wagner et al. (2001) and one genotype from the Oat Improvement Program at the University of Passo Fundo (UPF).

The parent generations (P_1 and P_2), F_1 and F_2 were studied in all crossings plus some others from the subsequent F_3, F_4, F_5, BC_1F_1, and BC_2F_1 generations, when possible in some of the crossings according to Table 2, 3 and 4. Seeds of all generations were obtained simultaneously from plants grown on the field.

The method we used to determine tolerance was the one proposed by Camargo and Oliveira (1981), which consists of one complete and one treatment solution. The complete solution contains all nutrients required for a normal development of the plant into which the evaluated genotypes were sown, and where they were returned to after having gone through the treatment solution. The treatment solution consisted of only a tenth of the complete solution plus an aluminum source.

By this method, the genotypes were first sown in complete solution, where they remained for 48 hours. Then they were transferred to the treatment solution containing toxic aluminum where they were kept for 48 hours. In the following, the genotypes were returned to the complete solution and kept there for 72 hours.

The seeds of the genotypes and segregating populations were size-standardized to minimize probable effects on the experimental error. The seeds of genotypes and segregating populations had previously been stored at temperatures of around 8º C for 10 days, to break dormancy and for the standardization of the germination. Thereafter they were husked and disinfested with 7% sodium hypochlorite for 5 minutes and then washed six times in distilled sterile water. The seeds were then placed to germinate on filter paper, moistened with distilled water, and put into a BOD incubator at 25º C, where they were kept for approximately 48 hours until the emission of approximately 5mm long rootlets.

Throughout the entire period, the plantlets were grown on plastic films adapted to lids of pots in constant contact with the nutrition solution. The pots with nutrition solution were placed in water bath tanks, where the water temperature was maintained at 20º C by resistances linked to the tank and to air conditioning. The light was maintained constant throughout all experiments, and the pots containing nutrition solution were connected to an oxygenation system.

The evaluation consisted of measuring regrowth of the main root of each plantlet when removed from the complete solution after the last 72 hours. Regrowth was measured based on the callosity caused when the plants were placed in the aluminum-containing solution that provokes root thickening and growth reduction or paralyzation. Tolerant plants, when placed in solution without aluminum again, began to develop normally anew, while the development of sensitive plants was affected or even paralyzed.

The complete nutrition solution was composed of 5 m M $CaCl_2$; 6.5 mM KNO_3; 2.5 mM $MgCl_2$; 0.1 mM $(NH_4)SO_4$; and 0.4 mM NH_4NO_3.

The solution treatment consisted of a tenth of the complete solution, plus 20ppm Al^{+++} in the form of $AlCl_3$. The pH of the solutions was previously adjusted to 4.0 with 0.1N HCl and daily readjusted to this level.

The observed growth was distributed in classes and the intervals determined according to the formula:

$i = A/K$

$K = \sqrt{n}$

where: i = class interval; A = range between the highest and smallest number, K = number of classes and n = number of observations.

A genetic hypothesis with respect to the number of segregating genes was tested for each population, based on the distribution of frequencies obtained in the generations and tested by the χ^2 test (Steel and Torrie 1960). Tolerant and sensitive classes were established according to the distribution of the classes of the parental genotypes and of the other studied generations.

The variances were calculated and the genetic effects estimated by the method of the generation mean of six crossings (UFRGS 17 x UFRGS 911715, UFRGS 17 x UFRGS 93598-6, UFRGS17 x UPF 91Al100-1-4, UFRGS 911715 x UFRGS 93598-6, UFRGS 911715 x UPF 91Al100-1-4, and UPF 91Al100-1-4 x UFRGS 93598-6).

The genetic effects of means, additivity and dominance were estimated based on data of the generations of each crossing and tested by the analysis of generation means, according to Mather and Jinks (1982).

This method allows the estimation of a lower number of parameters in a unit than the number of generations available. The three-parameter-model was tested for each crossing: mean (m), additivity (a) and dominance (d). The comparison of the fitting of models was realized by the χ^2 test with n degrees of freedom, which correspond to the difference between the number of available generations and the number of estimated parameters.

The environmental (V_E), genetic (V_G), additive (V_A) and phenotypic variances (V_P), as well as heritability in the broad sense (h_a) were estimated for the generations P_1, P_2, F_1, F_2, BC_1F_1, BC_2F_1, as these were obtained in the different crossings, using the formula proposed by Allard (1971) and the error of the heritability estimate according to Vello and Vencovsky (1974).

Table 1. Pedigree of the oat genotypes under study and their response to aluminum toxicity

Genotype	Pedigree	Response to aluminum
UFRGS 17	Cor²/CTZ³/PENDEK/ME1563//76-29/76-23/75-28/CI833	tolerant
UPF 91Al100-1-4	8014/301/SRcpx/CRcps/SRcpx/JHG-8	tolerant
UFRGS 911715	UFRGS 86A 1194-2/UFRGS8	intermediate
UFRGS 93598-6	UFRGS 15/UFRGS 881920	sensitive

RESULTS AND DISCUSSION

Results obtained in the comparisons between the resistant cultivar UFRGS 17 with a regrowth mean of 2.32 cm and cultivars UFRGS 911715 (intermediate), regrowth of 1.25 cm and sensitive UFRGS 95398 with mean regrowth of 0.60 cm are shown in Table 2. The hypothesis of a difference of one gene between the parents in the segregating generations was accepted by most of them. Only in the F_2 generation of crossing UFRGS 17 x UFRGS 93598-6 there was a higher number of sensitive plants than expected, while in the same crossing the results were adequate to the difference of one gene in the more advanced F_4 and F_5 generations.

Results obtained in the crossings between the resistant genotype UPF 91 Al 100-1-4 and the intermediate UFRGS 911715 and sensitive UFRGS 95398 are shown in Table 3. Mean values of regrowth of the parental genotypes (2.20, 1.70 and 0.60 cm) were very similar to those observed in the first group of crossings. frequencies in the further advanced generations, making the discrimination of the genotypes regarding the trait easier.

Other studies indicate that one or two genes are responsible for tolerance in wheat (Camargo 1984, Lagos et al. 1991, Camargo et al. 1992, Riede and Anderson 1996, Johnson Junior et al. 1997) and barley (Tang et al. 2000) and due to the existing synteny between these crops and oat it is possible that the aluminum tolerance genes could present a high degree of homology.

The additive-dominant model with three parameters was sufficient to explain the genetic effects present in the populations under study, even when leaving out the parameters that were not significant in the model, indicating that the epistatic effects were not important for the trait regrowth of the main root in these crossings (Table 5).

Additivity was significant in most of the crossings and only in crossing UFRGS 17 x UPF 91Al100-1-4, which was not contrasting for root regrowth, it was not significant. In all crossings involving the sensitive genotype UFRGS 93598-6, the interaction of dominance was however highly significant and always in the direction of tolerance, in line with the results obtained for the distribution of frequencies.

The results regarding tolerance to aluminum toxicity in oat have indicated that the model, with only three parameters, is insufficient to explain the obtained genetic variance (Sánchez-Chacón et al. 2000, Wagner et al. 2001). In this study however, the higher number of plantlets and greater uniformity of the initial root size of plantlets evaluated in nutritive solution must have contributed to an enhanced estimate of the effects in the study populations so the model with three parameters was sufficient to explain the obtained genetic variance.

The estimates of variances demonstrate that the genetic variance was higher than the environmental variance for most of the crossings. For the non-contrasting crossing for the trait, UFRGS 17 x UPF 91Al100-1-4 the variances were not estimated (Table 6). The broad-sense heritabilities were therefore high for most crossings.

The greatest importance of the additive gene action obtained in the genetic characterization of the studied genotypes indicates that the selection of genotypes and the incorporation of the trait in elite genotypes of improvement programs can easily be achieved. The simple inheritance of the trait and the high heritability observed in the contrasting crossings also reinforce this hypothesis.

Table 2. Distribution of frequency for regrowth of the main root of plantlets of different generations, for the crossings UFRGS 17 x UFRGS 911715 and UFRGS 17 x UFRGS 93598-6 and evaluation of segregation by the χ^2 test

UFRGS 17 x UFRGS 911715

Generation	Regrowth (cm)																	Total	Mean	Standard error	Variance
	0.2	0.4	0.6	0.8	1	1.2	1.4	1.6	1.8	2	2.2	2.4	2.6	2.8	3	3.2	3.4				
P_1									6	21	27	25	18	7	7	6		117	2.32	0.334	0.1113
P_2			1	12	19	61	54	40	1									188	1.25	0.23	0.0527
F_1							1	2	3	2	6	6	4		2			26	2.18	0.392	0.1538
F_2				4	16	44	47	25	36	71	75	61	25	10	5	7	4	430	1.90	0.536	0.2869
BC_1F_1										1	2	1	4	6	6	4	1	25	2.76	0.342	0.1167
F_5		5	9	18	22	26	19	5	24	30	17	6	2					183	1.43	0.54	0.2950

	Number of observed plants		Total	Expected Proportion	Value of ^{2}	Probability (P)
	Sensitive	Tolerant				
F_2	111	319	430	1:3	0.15	0.70
BC_1F_1	0	26	26	0:1	0.00	1.00
F_5	99	84	183	30:34	3.70	0.10 - 0.05

UFRGS 17 x UFRGS 93598-6

Generation	Regrowth (cm)																	Total	Mean	Standard error	Variance
	0.2	0.4	0.6	0.8	1	1.2	1.4	1.6	1.8	2	2.2	2.4	2.6	2.8	3	3.2	3.4				
P_1								1	6	17	27	27	19	8	4	3		112	2.31	0.329	0.1086
P_2	22	65	17	22	28	16	5	3										178	0.60	0.358	0.1279
F_1							1	2			3	3	3					12	2.13	0.44	0.1933
F_2	1	14	19	18	34	38	31	32	59	47	47	46	35	22	16	5	3	467	1.76	0.704	0.4956
F_4	1	1	5	9	18	23	25	9	14	15	18	18	13	4	2	1		176	1.64	0.631	0.3979
F_5		6	9	9	17	23	11	10	17	22	14	16	10	6	3	2		175	1.61	0.682	0.4649

Generation	Number of observed plants		Total	Expected Proportion	Value of ^{2}	Probability (P)
	Sensitive	Tolerant				
F_2	155	312	467	1:3	16.47	< 0.01
F_4	82	94	176	7:9	0.57	0.50 - 0.30
F_5	75	100	175	30:34	1.13	0.20 – 0.30

The selection of genotypes in segregating populations can be done in early generations, but, since the gene action of dominance was also significant, as observed in the analysis of frequency distribution, this selection should be accompanied by a progeny test for identification of homozygous lines for the gene of tolerance to aluminum toxicity.

Table 3. Distribution of frequency for regrowth of the main root of plantlets of different generations, for the crossings UPF 91Al100-1-4 x UFRGS 911715 and UPF 91Al100-1-4 x UFRGS 93598-6 and evaluation of the segregation by the χ^2 test

UPF 91Al100-1-4 x UFRGS 911715

Generation	Regrowth (cm)																	Total	Mean	Standard error	Variance
	0.2	0.4	0.6	0.8	1	1.2	1.4	1.6	1.8	2	2.2	2.4	2.6	2.8	3	3.2	3.4				
P_1									1	7	13	18	14	11	3	1	1	69	2.42	0.315	0.0992
P_2	1			3	12	15	11	11	3									56	1.22	0.290	0.0843
F_1							5	13	21	14	8	5	0	3				69	1.85	0.315	0.0995
F_2				10	12	34	30	19	39	59	46	38	15	5	5	3	1	316	1.8422	0.525	0.2751
RC_1F_1								2		4	3	5	4	1	2	2		23	2.38	0.452	0.2045

	Number of observed plants		Total	Expected Proportion	Value of χ^2	Probability (P)
	Sensitive	Tolerant				
F_2	86	230	316	1:3	0.83	0.50 - 0.30
RC_1F_1	0	23	23	0:1	0.00	1.00

UPF 91Al100-1-4 x UFRGS 93598-6

Generation	Regrowth (cm)																	Total	Mean	Standard error	Variance
	0.2	0.4	0.6	0.8	1	1.2	1.4	1.6	1.8	2	2.2	2.4	2.6	2.8	3	3.2	3.4				
P_1								1	15	12	9	5	2		1		2	47	2.06	0.389	0.151
P_2	4	18	11	12	8	1												54	0.56	0.264	0.0699
F_1								12	8	7	1			1				29	1.76	0.258	0.0668
F_2		9	12	11	12	17	21	16	56	41	29	20	7	14	4	4		273	1.72	0.6341	0.4021
RC_1F_1							5	9	6		2			1				23	1.66	0.3245	0.1053
RC_2F_1				3	1	1	2	3	5	2								17	1.42	0.4019	0.1615

Generation	Number of observed plants		Total	Expected Proportion	Value of χ^2	Probability (P)
	Sensitive	Tolerant				
F_2	82	191	273	1:3	3.8	0.10 – 0.05
RC_1F_1	0	23	23	0:1	0.00	1.00
RC_2F_1	7	10	17	1:1	0.52	0.50 – 0.30

Table 4. Distribution of frequency for regrowth of the main root of plantlets of different generations, for the crossing UFRGS 17 x UPF 91Al100-1-4 and UFRGS 93598-6 x UFRGS 911715 and evaluation of the segregation by the test χ^2

UFRGS 93598-6 x UFRGS 911715

Generation	Regrowth (cm)											Total	Mean	Standard error	Variance
	0.3	0.5	0.7	0.9	1.1	1.3	1.5	1.7	1.9	2.1	2.3				
P_1	30	8	6	1	3							48	0.41	0.2139	0.0458
P_2				6	5	8	11	4	5			39	1.33	0.2966	0.0880
F_1				9	6	7	4	3	2			31	1.23	0.3207	0.1029
F_2	11	15	23	29	35	18	17	19	15	7	1	190	1.11	0.4784	0.2289
RC_1F_1	10	6	4	3								23	0.47	0.205	0.0420

	Number of observed plants		Total	Expected Proportion	Value of χ^2	Probability (P)
	Sensitive	Tolerant				
F_2	49	141	190	1:3	0.027	0.90 - 0.80
RC_1F_1	20	3	23	1:1	12.56	< 0.01

UFRGS 17 x UPF 91Al100-1-4

Generation	Regrowth (cm)																	Total	Mean	Standard error	Variance
	0.2	0.4	0.6	0.8	1	1.2	1.4	1.6	1.8	2	2.2	2.4	2.6	2.8	3	3.2	3.4				
P_1								2	16	22	19	16	12	12	5		1	105	2.23	0.378	0.1427
F_1									3	8	7	8	3	1	1			31	2.21	0.276	0.076
RC_2F_1									12	11	20	18	9	11	9	4	1	95	2.35	0.410	0.1684

Table 5. Means of the generations P1, P_2, F_1, F_2, RC_1F_1 and RC_2F_1, number of seeds evaluated in each generation (in brackets), values of the genetic effects, of the Chi-square test (χ^2) and coefficient of variation, for the trait root regrowth obtained in six oat crossings

Generation or Parameter	UFRGS17 x UFRGS911715	UFRGS17 x UFRGS93598-6	UFRGS17 x UPF 91Al100-1-4	UFRGS911715 x UFRGS93598-6	UPF 91Al100-1-4 x UFRGS911715	UPF 91Al100-1-4 x UFRGS93598-6
P_1	2.76±0.24 (20)	2.47±0.29 (31)	2.56±0.32 (26)	1.33±0.30 (40)	2.56±0.34 (27)	1.94±0.21 (39)
P_2	1.31±0.31 (17)	0.45±0.23 (28)	2.58±0.48 (28)	0.41±0.21 (49)	1.18±0.38 (26)	0.55±0.28 (44)
F_1	2.16±0.42 (26)	2.13±0.44 (12)	2.77±0.29 (22)	1.23±0.32 (34)	1.84±0.32 (69)	1.76±0.26 (29)
F_2	2.07±0.61 (127)	1.75±0.65 (157)	2.43±0.41 (102)	1.11±0.48 (190)	1.93±0.56 (135)	1.56±0.53 (191)
RC_1F_1	2.74±0.34 (25)				2.38±0.45 (23)	1.66±0.32 (23)
RC_2F_1						1.42±0.40 (17)
m	2.06**±0.09	1.46**±0.01	2.52**±0.14	0.87**±0.02	1.89**±0.06	1.25**±0.08
[a]	0.75**±0.10	1.01**±0.01	0.01±0.15	0.46**±0.02	0.71**±0.06	0.65**±0.08
[d]	0.24±0.22	0.66*±0.03	0.20±0.21	0.36*±0.04	-0.008±0.10	0.50*±0.15
df	2	1	1	1	2	3
χ^2	0.5249	0.0053	0.2703	0.0136	0.1278	0.7139
P	0.77	0.94	0.59	0.91	0.94	0.87
CV	22.2	5.2	19.9	13.7	12.8	31.7

df: degrees of freedom; P: probability by the Chi-square test; *, ** significant at the level of 5% and 1% for the t test

Table 6. Values of the variance phenotypic (V_p), variance of the environment (V_E), variance genetic (V_G) and heritability in the broad-sense (h_a) for the regrowth of the main root in six populations of oat

Crossing	V_P	V_E	V_G	h_a
UFRGS 17 x UFRGS 911715	0.29	0.11	0,18	0.62± 0.062
UFRGS 17 x UFRGS 93598-6	0.50	0.14	0.36	0.72 ± 0.060
UPF 91Al100-1-4 x UFRGS 911715	0.28	0.09	0.19	0.66 ± 0.053
UPF 91Al100-1-4 x UFRGS 93598-6	0.40	0.10	0.30	0.75 ± 0.053
UFRGS 911715 x UFRGS 93598-6	0.23	0.08	0.15	0.66 ± 0.071

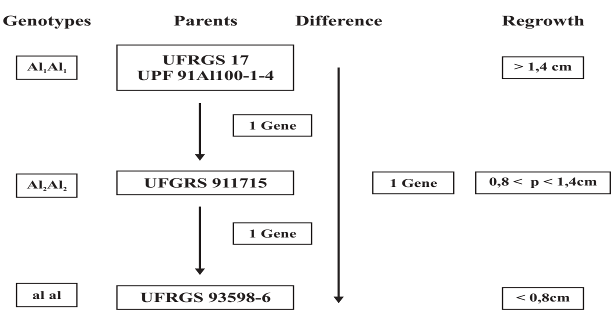

Figure 1. Diagram of differences between numbers of genes in oat genotypes

CONCLUSIONS

- The trait aluminum tolerance is genetically inheritable controlled by one gene with multiple alleles and genetic interaction of dominance for the tolerance in the studied populations.
- The broad-sense heritability estimate of the trait is high.
- Genotypes UFRGS 17 and UPF 91Al100-1-4 present one gene of tolerance to aluminum toxicity, with similar expression.
- The additive genetic effects and effects of dominance are important for the determination of the trait.

Herança da tolerância à toxicidade do alumínio do solo em aveia (*Avena sativa* L.)

RESUMO - *A toxicidade do alumínio é fator limitante para a expressão do potencial de rendimento na cultura da aveia. O desenvolvimento de genótipos tolerantes à toxidez ao alumínio é a alternativa mais barata e viável para o cultivo em solos com subsolo ácido. Os objetivos deste estudo foram: determinar a ação gênica, o número de genes e a herdabilidade da tolerância ao alumínio em genótipos de aveia. Genótipos parentais e as gerações F_1, F_2 e para alguns cruzamentos mais as gerações F_3, F_4, F_5, RC_1F_1 e RC_2F_1 foram discriminados através da análise do recrescimento da raiz de plântulas submetidas ao alumínio. A ação gênica aditiva foi a de maior importância e a segregação foi de apenas um gene com alelos múltiplos, sendo dois para tolerância (Al_1 e Al_2) e um para sensibilidade (al). A herdabilidade da característica foi alta, evidenciando que este caráter pode ser selecionado nas gerações iniciais nos programas de melhoramento.*

Palavras-chave: *Melhoramento de aveia, solos ácidos, raízes, genótipos, herdabilidade.*

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